RESEARCH PAPER

Seed germination and seedling establishment of Neotropical dry forest species in response to temperature and light conditions

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Abstract: A study was conducted to examine the germination requirements of *Cedrela odorata*, *Guaiacum sanctum* and *Calycophyllum candidissimum* seeds, and the effect of light intensity on survival and growth of *C. odorata* and *G. sanctum* seedlings planted on open, partially-open and beneath the canopy of a dry forest in Nicaragua. The results show that germination of *C. candidissimum* seeds was significantly higher in light than darkness at constant temperatures ranging from 20–35ºC. Both *C. odorata* and *G. sanctum* seeds germinated in light and darkness to a varying extent, and the optimal germination temperature was around 20-25ºC. Alternating temperature regimes did not improve germination. Survival of *G. sanctum* seedlings was 70% beneath the canopy and 80% in the open, and its relative growth rate in collar diameter was 1.88 mm/month in the open and 1.42 mm/month in the understory. Survival was generally poor for *C. odorata*, particularly in the understory. We concluded that light is an absolute requirement for the germination of *C. candidissimum* seeds while germination of *C. odorata* and *G. sanctum* seeds are more sensitive to temperature. Owing to its high survival rate on open site, *G. sanctum* could serve as a candidate species for reforestation of degraded sites.

Keywords: canopy cover; seed germination; Nicaragua; photoblastic seed; survival rate; restoration; *Cedrela odorata*; *Guaiacum sanctum*; *Calycophyllum candidissimum*

Introduction

Depletion of Neotropical dry forests, the associated loss of biodiversity, and the need for restoration of dry forests are well recognized today (Janzen 2002). Currently, large tracts of agricultural fields are being abandoned due to a shift in the economic interest in many parts of Central and Latin America (Thomlinson et al. 1996; Jansen 2002). In the past, such abandoned fields have largely been neglected. However, tropical secondary forests derived from abandoned fields have gained much attention in recent years owing to their socio-economic and ecological importance, their fast-growing properties and the current pressure on remaining old-growth forests (Guariguata and Ostertag 2001).

The major limitation for forest regeneration on abandoned

sites is seed availability, thus supplementary measures are often recommended to foster the recovery of woody vegetation (Zimmerman et al. 2000; Wijdeven and Kuzee 2000). One approach to expedite the recovery process is direct seeding of early successional species that in turn facilitates the establishment of late successional species. The other approach is planting framework species – are species with high survival and growth rates in the open degraded sites, develop dense spreading crowns that rapidly shade out herbaceous plants and provide resources for wildlife at an early stage (Goosem and Tucker 1995). In both cases, knowledge of seed germination and subsequent establishment and growth of seedlings is a prerequisite, as they are demographically critical phases in the regeneration of plants from seeds (Gerhardt 1996a).

In a country like Nicaragua where information is generally lacking for native tree species, the first step to forest restoration would be to carry out an extensive background study, ranging from seed germination to seedling establishment and growth in changing environment on degraded open sites. Open sites often experience high light intensity, low surface soil moisture and fluctuation in diurnal temperature (Bullock 2000) compared to the forest understory environment, depending on the canopy architecture (Lemenih et al. 2004). For non-dormant seed populations, temperature and light conditions play an important role in seed germination provided that enough soil moisture and aeration exist. Studies on dry forest species have shown large interspecific variation in the optimal temperature for germination (Teketay and Granström 1997; Tigabu and Odén 2001; Khurana

and Singh 2001; Zida et al. 2005). Light intensity and its spectral quality also markedly influence the germination, and survival and growth of seedlings of tropical tree species with marked interspecific variation (Rincon and Huante 1993; Ray and Brown 1995; Guariguata 2000;).

Three species from a tropical dry forest of Nicaragua, *Cedrela odorata* L., *Guaiacum sanctum* L. and *Calycophyllum candidissimum* (Vahl) DC, were investigated in the present study. The species were selected based on their economic, social and ecological significances. *C. odorata*, commonly known as Cedro, is a big tree that attains a height of 12–30 m and a dbh of 60–150 cm. The species naturally occurs from Mexico to South America. In Nicaragua, Cedro is found in low elevations with dry to very humid climate. It is also frequently found in grassland and cropland as isolated tree. It is generally found in the whole country forming small groups. Cedro is very important timber species owing to its high wood quality (Salas 1993) and regenerates poorly under natural conditions (González-Rivas 2005). *C. candidissimum*, commonly known as Madroño, is a pioneer tree that grows as tall as 6–30 m and to a dbh of 25–60 cm. Its natural distribution extends from Southern Mexico to Venezuela and Colombia. In Nicaragua, this species is found in dry and semi-humid areas, mainly in the Pacific coast and central region. *C. candidissimum* was declared as the National Tree of Nicaragua in 1971 (Salas 1993). *G. sanctum* is a slow-growing, small to medium tree that reaches 4 to 25 m in height and up to 60 cm dbh. It is largely confined to dry exposed sites and often dominates the vegetation. Its natural distribution extends from the Greater Antilles to southern Florida, eastern Mexico, along the west coast of Central America, to northern South America at elevations ranging from 10 to 200 m a.s.l in Costa Rica and up to 700 m in Nicaragua. It is limited to lowland deciduous dry tropical forest (Marín et al. 1999). *G. sanctum* is considered an endangered species in Nicaragua.

The objectives of this study were to (1) examine the germination responses of these species to different temperature regimes and light conditions, and (2) evaluate survival and growth of planted seedlings of *C. odorata* and *G. sanctum* over one year on open site, partially-open site and under closed canopy. As the species differ in their ecology from pioneer to late successional, it was hypothesized that seed germination and seedling establishment of these species would be different in response to temperature and light conditions.

Materials and methods

Seed sources

Seeds of the studied species were purchased from Semillas Forestales del Trópico (Tropical Forest Seeds) company in Diriamba, Carazo, Nicaragua. Seeds of *C. odorata* and *C. candidissimum* were collected from Ometepe Island and seeds of *G. sanctum* were collected from Sabana Verde, Sébaco, Nicaragua in 2004. *C. candidissimum* has the smallest seeds, followed by *C. odorata* and *G. sanctum*, respectively (Table 1). Seeds were packed in plastic bags and transported to the Swedish University of Agri-

cultural Sciences, Department of Silviculture, Umeå where the germination experiment was conducted. They were stored for ca. three weeks at 5°C until the study was carried out.

Table 1. Seed morphological characteristics and initial seedling size at the time of planting for three dry forest species

Species	Seed traits			Seedling traits	
	Length (cm)	Width (cm)	Seed mass (g)	Diameter (mm)	Height (cm)
C. odorata	1.0 ± 0.3	0.4 ± 0.2	0.02 ± 0.01	3.4 ± 0.12	15.1 ± 0.59
G. sanctum	0.9 ± 0.2	0.4 ± 0.2	0.18 ± 0.05	1.9 ± 0.14	13.7 ± 0.58
C. candidissimum	0.3 ± 0.1	0.1 ± 0.04	0.0003 ± 0.0001	*	*

* not included in the seedling establishment experiment (see methods)

Seed germination

A 7 × 2 factorial experiment was set-up to examine the effects of different temperature regimes and light conditions on seed germination of three dry forest species. The temperature regime had seven levels: five constant temperatures from 15–35°C at an interval of 5°C and two fluctuating temperature, 20/15°C and 25/15°C with a thermoperiod of 12 h. Although the temperature of the study site ranges between 20°C and 30°C with a mean of 26°C (González-Rivas 2005), the lower and the higher temperature regimes (15°C and 35°C) were included in the present test to get an insight about the theoretical minimum and maximum germination temperature. The light condition had two levels: continuous exposure to constant light (20 µE·m⁻²·s⁻¹, fluorescent lamp F40 W/33 RS cool white light) for 24 h and complete darkness. As seeds of these species are not dormant, pretreatments were not applied.

The germination test was performed on plates with pits using standard germination paper (Munktell analytical filter paper, 75 mm diameter) as germination substrate. Each germination plate had 12 pits and the size of each pit was 7 cm in diameter and 3 cm in depth. Each pit was filled with de-ionized water and covered with aluminum foil with a slot in the middle. One piece of germination paper, also with a slot, was placed on the aluminum foil. Two strips of narrow germination paper were inserted through the slots of the germination paper and the aluminum foil into the de-ionized water in the pit to act as wicks. Another piece of germination paper with 25 seeds per replication was placed on top. Each set of seeds was then covered with a bell jar (black jars for dark experiments and white transparent jars for light experiments) with a hole at the side to allow gas exchange. Such an arrangement enabled seeds to uptake water continuously throughout the test period without disturbing the experiment, especially the dark experiment. The germination plates were put in growth chambers set at the specified temperature regimes. For each studied species, a total of 100 seeds, four replicates of 25 seeds each, were used in each treatment. The germination test was run for 21 days. The germination process was monitored every day for seeds incubated in continuous light and germinated seeds were counted when the radicle reached 2 mm and had normal appearance. For dark incubated seeds, the final germination count was made after 21 days.

Seedling establishment

The seedling establishment experiment involved two species, *C. odorata* and *G. sanctum*, as seeds of *C. candidissimum* were scarce during the time of seedling production in the nursery. Seedlings were raised in the Ministry of Natural Resources and Environment nursery in Managua, Nicaragua. After six months, the seedlings were outplanted under three canopy cover conditions, 0% (open site), 50% (partially-open site) and 100% (closed canopy), in the dry deciduous forest of Chacocente National Wildlife Refugee in August 2003 (the main rainy season). The dry forests of Chacocente, the remaining moderately disturbed forest in Nicaragua, is located at 11°30′–11°36′N and 86°08′–86°15′ W along the Pacific coast. The mean annual precipitation and temperature for the period 1981–2001 was 1431 ± 369 mm and 26.6 ± 0.34°C, and the dry period spans over five months, from December to April. Soils in this forest are classified as Vertic and Ferric Luvisol (Sabogal and Valerio 1998). Plots were systematically selected to represent the different canopy cover, which was determined using a spherical densiometer. For each species, a total of 20 seedlings were planted at a spacing of 1 m × 1 m. Each individual seedling was tagged, and the height and root collar diameter were measured at planting (Table 1). Seedlings were re-measured one year later in August 2004 to evaluate survival and growth.

Data analyses

For the germination experiment, germination capacity (GC) and mean germination time (MGT) were calculated for each treatment as follows:

$$GC \ (\%) \ = \ \frac{\left(\sum n_i\right)}{N} \times 100 \tag{1}$$

$$MGT \ (days) \ = \ \frac{\sum (t_i n_i)}{\sum n_i} \tag{2}$$

where t_i is the number of day starting from the day of sowing, n_i is the numbers of seeds germinated at each day and N is the total number of seeds sown per replicate. The germination data sets were arcsine transformed before analysis (Zar 1996) and two-way ANOVA was performed to determine whether GC varies among temperature regimes and light conditions for each species separately. For statistical analysis, the MGT was considered for species and treatments that showed some germination in all the replicates and One-way ANOVA was used to test the main effect of temperature regimes on MGT. Means that showed significant differences were compared using Tukey's test at the 5% level of significance.

For the seedling establishment experiment, survival, height and root collar diameter were assessed after one year. A Chi-square analysis of 2 × 3 contingency table was performed to test the null hypothesis that seedling survival is independent of the density of canopy cover. As survival of *C. odorata* seedlings was

extremely low, the growth rate (GR) in root collar diameter was computed for *G. sanctum* only. GR was computed using the following equation:

$$GR \ = \ \left(\frac{\ln D_2 - \ln D_1}{\Delta t}\right) \tag{3}$$

where, D_2 and D_1 are the diameter at the time of planting and after one year, respectively and Δt is the time interval between two measurements. One-way ANOVA with unequal number of replication (n = 16, 16 and 14 for open, partially-open and closed canopy, respectively) was performed to examine differences in GR in collar diameter in relation to the density of canopy cover using each individual seedling as replicate. GR in height was not computed for any of the species, as the majority of individual seedlings were clipped by herbivores, resulting in negative growth rate.

Results

Seed germination

The GC of seeds of species tested in the present study varied significantly in response to different temperature regimes, light conditions, and for the interaction terms (p < 0.0001). Under continuous exposure to light, seeds of *C. candidissimum* had the highest GC when incubated at constant temperatures ranging from 20°C to 35°C while no germination was occurred at 15°C (Fig. 1A). Germination was significantly inhibited in darkness at all constant temperature regimes. Seeds of *G. sanctum* germinated equally well in light and darkness, but the GC was strongly dependent on temperature (Fig.1B). Under continuous exposure to light, the GC of *G. sanctum* seeds was significantly higher when incubated at 20°C and 25°C than at 15°C and 35°C (p < 0.001). Up to 61% of seeds incubated at 30°C in darkness germinated but none germinated in light. Alternating temperature regimes did not result in germination either in light or darkness. The overall GC of *C. odorata* was generally lower than that of the other two species. Seeds exposed to continuous light had significantly higher GC than dark incubated seeds, especially at 20°C, 25°C and 35°C (Fig. 1C). Alternating temperature regimes completely inhibited the germination of seeds of all species irrespective of light conditions.

The speed of germination, as determined by the MGT, also showed significant differences among temperature regimes for all the species (p < 0.001 for *C. odorata*; p = 0.007 for *C. candidissimum*; p = 0.001 for *G. sanctum*; Table 2). Seeds of *C. odorata* incubated at 15°C germinated slowly compared to other constant temperature regimes. For *G. sanctum* seeds, germination was fastest at 25°C followed by 20°C. The MGT for *C. candidissimum* seeds was significantly different among constant temperature regimes, but showed a narrower range. The overall speed of germination in *C. candidissimum* across the range of constant temperatures was generally faster than for the other species.

Table 2. Mean germination time (days) of seeds of three tropical dry forest species germinated under different constant temperature regimes in light (mean ± SE).

Species	Mean germination time (days) under different temperatures				
	15ºC	20ºC	25ºC	30ºC	35ºC
C. odorata	13.9 ± 1.5 a (28)	6.1 ± 0.4 b (56)	4.4 ± 0.3 b (59)	5.0 ± 0.4 b (42)	4.4 ± 0.3 b (54)
C. candidissimum	* (0)	5.4 ± 0.1 a (90)	4.1 ± 0.1 b (92)	4.4 ± 0.2 b (94)	4.6 ± 0.3 ab (93)
G. sanctum	18.5 ± 2.5 a (4)	9.9 ± 1.2 bc (80)	6.4 ± 0.58 c (82)	* (0.0)	15.5 ± 1.8 ab (33)

* Computation of mean germination time was not possible because no seeds germinated. Means followed by the same letter within the column are not significantly different using Tukey's test (p = 0.05). Total number of germinated seeds per treatment is given in parenthesis.
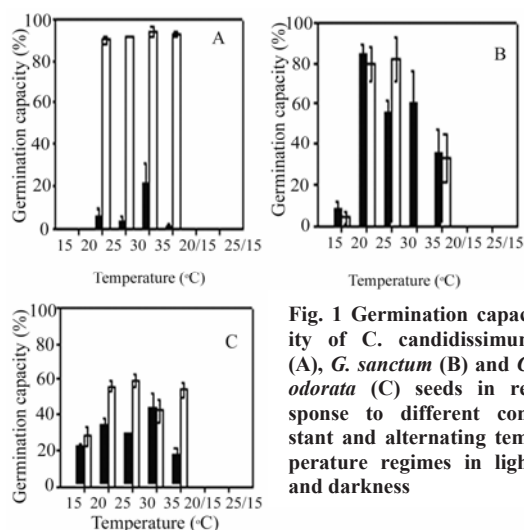
Fig. 1 Germination capacity of C. candidissimum (A), G. sanctum (B) and C. odorata (C) seeds in response to different constant and alternating temperature regimes in light and darkness

Seedling establishment

Survival of transplanted seedlings was strongly dependent on the density of canopy cover ($x^2_{(0.05, 2)}$ = 20.843; p < 0.0001) and varied among species. Seedlings of G. sanctum had the highest survivorship in all sites while C. odorata did not survive under the canopy (Fig. 2A). As a whole, G. sanctum seedlings survived better than C. odorata. For G. sanctum, the growth rate in collar diameter varied significantly among sites (P< 0.001). It ranged from 1.88 mm/month in the open site to 1.42 mm/month under the canopy (Fig. 2B). The growth rate was not calculated for C. odorata because of high mortality.
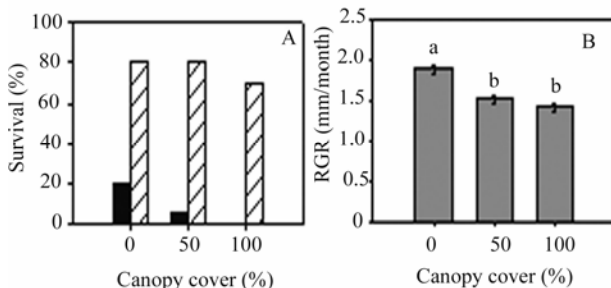
Fig. 2 Survival of C. odorata (shaded bar) and G. sanctum (striped bar) seedlings (A), and relative growth rate (RGR) in root collar diameter of G. sanctum seedlings (B) planted under different canopy cover in Chacocente dry deciduous forest, Nicaragua. Letters on the graph denote significant difference in RGR (p < 0.05).

Discussion

The species tested in the present study exhibited a distinct dichotomy with respect to light requirement for germination. The germination of seeds of C. candidissimum and C. odorata was generally higher when incubated in light than in darkness while seeds of G. sanctum germinated well both in light and darkness, although the light requirement was modulated by temperature. C. candidissimum is a pioneer species producing a large quantity of small seeds due to highly synchronized flowering with little annual variation (Rivera and Borchert 2001). Photoblastic germination is typical characteristic of pioneer species known to have small seeds (Teketay and Granström 1997; Milberg et al. 2000; Pearson et al. 2002, 2003). The ecological significance of photoblastic germination is interpreted as a mechanism for detecting gap formation or disturbance on the forest floor, as the red/far red ratio has been shown to increase appreciably following such disturbances (Vázguez-Yanes et al. 1990; Vázguez-Yanes and Orozco-Segovia 1992; Pons 2000). This, in turn, enables these pioneer species to rapidly colonize newly disturbed sites (Teketay and Granström 1997; Teketay 1998b). Another ecological benefit associated with the production of small seeds in large quantity is a better chance to enter into the soil easily than large seeds and thus facilitate the build-up of a persistent seed bank, essential for regeneration of species following disturbance (Teketay and Granström 1995; Thompson 2000).

The effect of different temperature regimes on germination varied among species tested in the present study. For all species, seeds incubated under alternating temperature regimes did not germinate. Sensitivity to alternating temperature depends on amplitude (the difference between the maximum and minimum temperature), thermoperiod (time in hours each day above the mean temperature) and number of temperature cycles (Ekstam et al. 1999; Probert 2000). In some species, germination declines with increasing amplitude (Teketay and Granström 1997) while it increases in other species (Thompson and Grime 1983). The sensitivity of seed populations to alternating temperature may also interact with other environmental factors, particularly light . Some light-requiring species germinate well under alternating temperatures with varying amplitudes in darkness (Teketay and Granström 1997). This suggests that each species has optimum amplitude for triggering germination. As the fluctuating temperature regimes in the natural habitat are far more complex than those tested in this study, the potential positive effect of fluctuating temperature on germination of these species, particularly the light-requiring species (C. candidissimum), in their natural habi-

tats cannot be ruled out.

The optimum temperature for germination varied considerably among species. Seeds of *C. candidissimum* had higher germination than the other two species at all constant temperature regimes, except 15°C under continuous exposure to light. The optimal germination temperatures for *G. sanctum* were at 20 and 25°C. For *C. odorata* seeds, germination was higher at 20°C, 25°C and 35°C than 15°C and 30°C. The germination of *G. sanctum* seeds was also relatively high when incubated at 20°C in darkness, and that of *C. odorata* was high at 30°C in darkness. Germination of *C. odorata* seeds was relatively higher at 15°C in both continuous light and darkness than the other two species. This could be related to induction of secondary dormancy, as seeds remaining ungerminated were still intact (per. obs). A similar finding has been reported for *Moringa stenopetala* where seeds initially placed at 10°C and 15°C did not germinate but as high as 58% and 70% germination were recorded when they were transferred to 20°C and 25°C, respectively (Teketay 1995). A complete failure of *G. sanctum* seeds to germinate at 30°C under continuous exposure to light could be linked to frequent and rapid drying of the germination papers for unknown reason (per. obs.). As a whole, the optimal temperature ranges found in this study is typical for many other tropical tree species (Teketay and Granström 1997; Tigabu and Odén 2001; Zida et al. 2005).

Seedling survival and growth

Survival of planted seedlings varied considerably between species. Regardless of the density of canopy cover, survivorship was much higher for *G. sanctum* than *C. odorata* seedlings. Variation in seedling mortality among species depends on the size and age of seedlings and the soft tissue required for their rapid development (Kitajima and Fenner 2000). Young seedlings are highly susceptible to biotic and abiotic stress, such as herbivory, disease, water stress, and physical damage induced by litter fall (Gerhardt 1998; Scariot 2000; Sherman 2002). Gerhardt (1996b) has found a positive correlation between survival and initial seedling size. The large size of survived seedlings of *G. sanctum* may partly explain their high survival rate compared with *C. odorata*.

Survival of *C. odorata* was relatively better in the open site than under the canopy. Previous studies made on dry forest species have reported a drastic decline in survival of planted seedlings after one year under the forest canopy compared with open sites (Guariguata 2000). Poor survival under closed canopy is a direct consequence of low light intensity, particularly for light-demanding pioneer species like *C. odorata*. Shading has also been shown to increase seedling mortality indirectly by exacerbating fungal attack through increased humidity or by providing concealment for seedling predators (Sherman 2002). Gerhardt (1998) also suggested that the lower survival rate of *C. odorata* seedlings transplanted in the secondary forests in Guanacaste, Costa Rica is due to herbivory combined with drought. Similarly, we observed signs of browsing damage on *C. odorata* and *G. sanctum* seedlings, most likely by both wild and domestic herbivores, during the time of assessment. Although *C. candidissimum* was not included in the seedling survival study, the sur-

vival of naturally regenerated seedlings was higher under shade (González-Rivas 2005). It is interesting to note that this species exhibits distinct light requirement for seed germination and seedling establishment. This suggests that not only light but also other environmental factors govern the subsequent establishment of tree species in dry environments. Soil moisture availability is a key factor influencing the growth and survival of plant communities in tropical dry forests. For Caribbean dry forest species, Ray and Brown (1995) suggested that survival of young seedlings are closely linked to rainfall quantity and timing, and seedling desiccation may indeed be a major obstacle to recruitment.

Growth of *G. sanctum* seedlings was more favored in open than closed canopy, as evidenced by the significantly higher growth rate in root collar diameter. This could be related to reduction in competition for one or more resources in the open relative to closed canopy. For example, reduction of competition along the root zone using trenching has shown to increase seedling growth in the deciduous forest (Gerhardt 1996b). For many tropical deciduous species of Mexico, growth rate and net assimilation rates are higher in high light treatment than at low light intensity similar to that found underneath the canopy (Rincon and Huante 1993).

Conclusions

The results presented here illustrate that light is an absolute requirement for the germination of *C. candidissimum* seeds. Seed of this species also germinated in a wide range of constant temperature regimes. Therefore excessive shading of nursery seed beds, deep sowing and covering with leaf litter during direct seeding in the field or nursery should be avoided. Dark germination of *C. odorata* seeds was lower than germination in light, and germination was higher in narrow temperature range (20-25°C). Medium shading of nursery seed beds and the use of mulches for seeds sown directly in the field will benefit seed germination by lowering the temperature in dry areas like Nicaragua. Temperature is more important for the germination of *G. sanctum* seeds than light. Regulating temperature using covers/shades both in the nursery and in the field would be beneficial. Planted seedlings of *G. sanctum* have good survival and growth on open and partially-open sites. Thus, this species could serve as a candidate species for mixed planting on degraded areas as well as for enrichment planting of disturbed dry forests. Survival of *C. odorata* was low in open and partially-open sites and seedlings failed to survival under the canopy of dry deciduous forest in Nicaragua, most likely due to its sensitivity to drought and browsing damage. Therefore, the use of mulching during planting to conserve moisture and utmost protection of damage at the early phase of establishment would be advisable to enhance establishment success.

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